

THE ALSOPHILA SWARTZIANA COMPLEX (CYATHEACEAE).*

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The genus *Alsophila* R. Brown comprises about 350 species, widely distributed in the tropical and subtropicals regions of the world, with about 150 species in America. This genus can be distinguished from the others of the family, in a traditional sense, by the stem and petioles with scales, and the sori without an indusium or with only a minute scale-like indusium. In a more restricted sense it would include only such species of the traditional genus as have flabelloid petiole scales. The group of *Alsophila swartziana* falls under *Alsophila* in either classification.

I agree with Holttum, (1957), who considers that the morphology of the petiole scales is a character to define natural groups in this family. Holttum recognized two basic types of scales: setiferous scales, with marginal denticulations bicolorous or concolorous with the entire body of the scale, and flabelloid scales, with a margin formed by very fragile cells, very different from the cells of the body of the scale. In the American species of the genera of tree-ferns, however, the structure presented by the petiole scales is more complicated and more diverse than a setiferous type and a flabelloid type.

Maxon (1922) established an informal group of species related to *Alsophila armata* (= *A. swartziana*) based principally on the complete absence of indusium, the degree and type of dissection of the leaf and the pubescence. The South American members of this group were not treated. In the

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present paper other characteristics of the petiole scales have been used to define the group, in addition to those employed by Maxon, and five species must be excluded from the group: *A. microdonta*, *A. myosuroides*, *A. notabilis*, *A. mexicana* and *A. acutidens*. It includes the American species of *Alsophila* with subflabelloid scales in which the border is more or less differentiated and the margin of the petiole scales of mature leaves or croziers has dark denticulations (fig. 1). The group of *Alsophila swartziana*, then, includes three species of the West Indies, five of Mexico and Central America, four South American species, and a single one of both Central and South America.

KEY TO THE SPECIES

- a. Veins of the fertile segments simple, or once forked near the border of the segment; sori borne below the branching of the vein; Jamaica. 1. *A. estelae*
- a. Veins of the fertile segments medially forked at least once; sori borne at the branching of the vein. b.
- b. Petiole abundantly pubescent, the trichomes sometimes deciduous and then leaving a hard elevated base and a scabrous surface (smooth in *A. swartziana* of the Greater Antilles). c.
- c. Paraphyses turgid, persistent, dark red and shorter than the sporangia; Cocos Island. 2. *A. nesiotica*
- c. Paraphyses slender, obtuse or acute at the tip, deciduous or persistent, longer than the sporangia. d.
- d. Upper surface of the segments with abundant trichomes on the costules, veins and between the veins. e.
- e. Margin of petiole scales dark denticulate throughout; apex of pinnules long-attenuate, often curved; Costa Rica to Ecuador. 3. *A. trichiata*
- e. Margin of petiole scales smooth or with a few dark teeth apically; apex of pinnules acuminate, nearly straight; Venezuela, Colombia to Bolivia. 4. *A. tryonorum*
- d. Upper surface of the segments glabrous or with trichomes only on the costules and veins. f.
- f. Upper surface of veins with trichomes (when deciduous the bases evident); mature pinnules with few or no bulate scales along the costa beneath; Mexico to Honduras. g. 5. *A. scabriuscula*
- g. Sinuses of segments quadrangular in the basal portion of the pinnules; Mexico, Guatemala, Honduras. 5a. var. *scabriuscula*

- g. Sinuses of segments acute to rounded in the basal portion of the pinnules; Guatemala. 5b. var. *guatemalensis*
- f. Upper surface of veins glabrous; pinnules beneath with abundant bullate scales along the costa; a flattish scale nearly always present between the costule and the fork of the vein; Jamaica, Haiti and Dominican Republic. 6. *A. swartziana*
- b. Petioles glabrous or sparsely pubescent; the trichomes sometimes deciduous and then leaving a prominent scar and a nearly smooth surface. h.
- h. Pubescence of lower surface of the costa and costules only of abundant, flexuous, catenate reddish trichomes; eastern Cuba. 7. *A. strigillosa*
- h. Pubescence of lower surface of the costa and costules principally of abundant, stiff, terete trichomes. i.
- i. Petiole scales with a white body, or with a dark area only at the base; southeastern Brazil. j.
- j. Rachis glabrous, prickly with sparse slender spines, slightly hirsute at the apex; segments lanceolate, acute; fertile and sterile veins once forked. 8. *A. hirsuta*
- j. Rachis pubescent or subglabrous, unarmed; segments linear, obtuse or acute; fertile and sterile veins with one or two pinnate pairs of veinlets. 9. *A. rufa*
- i. Petiole scales, or most of them, with a narrow or broad, dark central stripe and a white border. k.
- k. Margin of the petiole scales smooth or with a few dark teeth apically or with a few marginal cells slightly darker than the others; veins impressed above; Colombia to Bolivia. 10. *A. conjugata*
- k. Margin of the petiole scales dark denticulate throughout; veins not impressed above. l.
- l. Rachis without spines, sometimes slightly muricate; lower surface of costules with flexuous trichomes; upper surface of costules and veins with thin and flexuous trichomes; Costa Rica and Panama. 11. *A. stipularis*
- l. Rachis with scattered, small, sharp spines; lower surface of costules with stiff trichomes; upper surface of segments glabrous or glabrescent. m.
- m. Petiole scales with continuous dark teeth along the margin, with a broad dark central stripe; Guatemala. 12. *A. pansamalana*
- m. Petiole scales with whitish cells between the dark teeth along the margin, with a narrow dark central

stripe or sometimes with a dark area at the base;
Mexico. 13. *A. bicrenata*

TAXONOMIC AND GEOGRAPHIC NOTES ON THE SPECIES.

1. ***Alsophila estelae*** Riba, *Rhodora* 69: 67, f. 5-7. 1967.

Type: Mount Horeb, Blue Mountains, Jamaica, *Riba 214* (MEXU); Isotype: (GH)

Alsophila estelae is endemic to Jamaica and is one of the most graceful tree-ferns of that island. At first sight it can be easily confused with *A. swartziana*, a species that grows in the same places. However, the slender trunk (3-4 m tall and ca. 4-6 cm thick) and the crown of small leaves make it a distinctive species in the field. *Alsophila estelae* has been collected only three times in Portland and St. Thomas Parishes.

2. ***Alsophila nesiotica*** Maxon, *Contrib. U. S. Nat. Herb* 24: 43. 1922.

Type: Cocos Island, Costa Rica, *Pittier 16229* (US).

The affinity of *Alsophila nesiotica* with the other species in this group is uncertain. The petiole scales do not have the margin dark denticulate, but the border is well differentiated, its cells are smaller than those of the center and are oriented in a fan-like manner, and a few marginal cells at the apex are slightly darker than the others, without any differentiation in teeth. Material of the croziers has not been available, but it is anticipated that they will have dark denticulate scales, as in *A. conjugata* and *A. tryonorum*.

This species grows only on Cocos Island, Costa Rica, where it has been collected four times.

3. ***Alsophila trichiata*** Maxon, *Contrib. U. S. Nat. Herb.* 24: 44, t. 15. 1922.

Type: Cana, Panama, *R. S. Williams 928* (US).

Alsophila trichiata (fig. 3) is a species which grows at low elevations, from almost sea level in Costa Rica and Panama and northern Venezuela, up to near 1,000 m of altitude in Ecuador. This species is related to *A. tryonorum*, but that species grows at higher elevations (up to 2,800 m) and

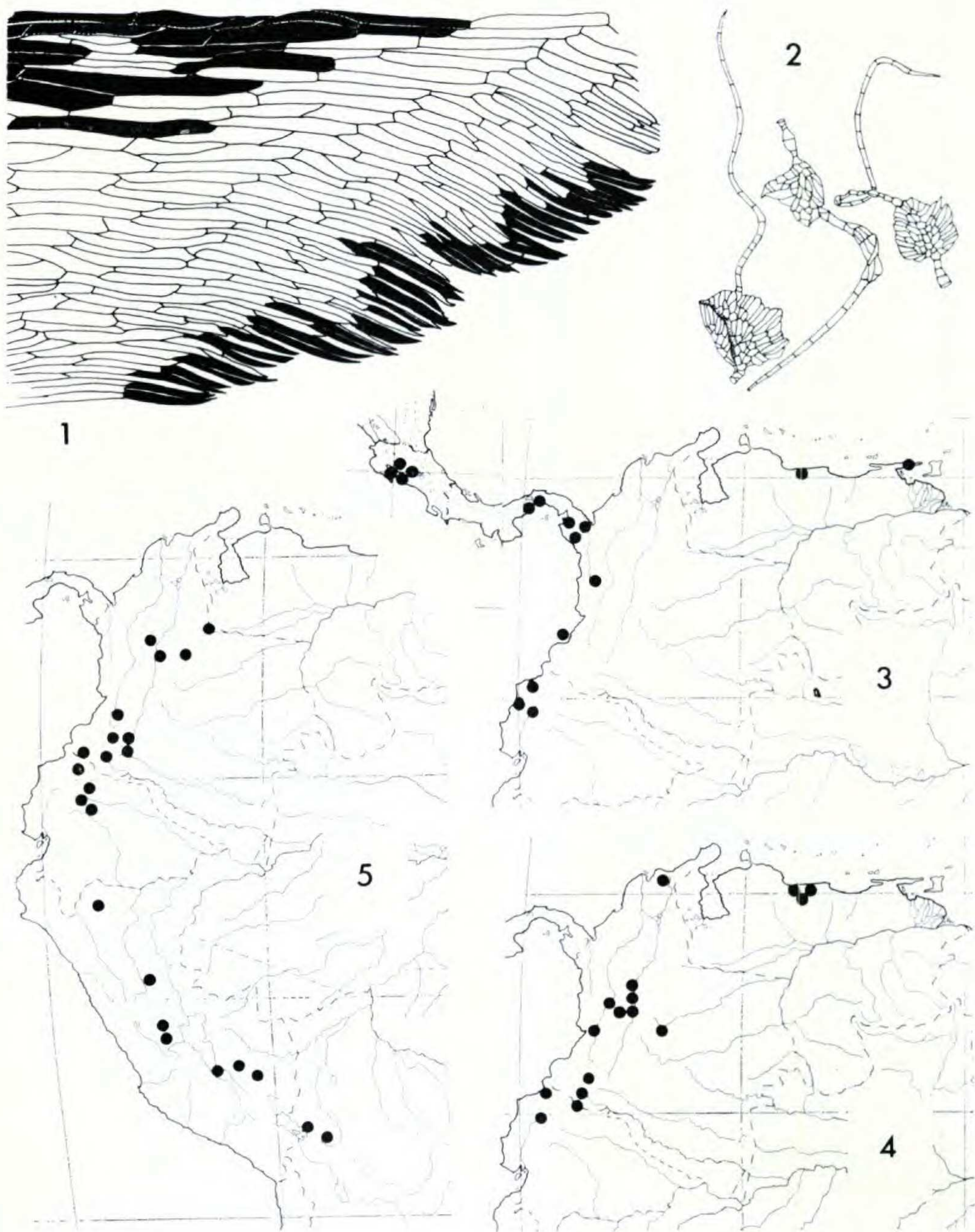


Fig. 1. Border of petiole scale of *Alsophila trichiata*, $\times 25$.
 Fig. 2. Winged trichomes from lower surface of costa of *Alsophila pansamalana*, $\times 40$. Fig. 3. Distribution of *Alsophila trichiata*.
 Fig. 4. Distribution of *Alsophila tryonorum*. Fig. 5. Distribution of *Alsophila conjugata*.

is easily distinguished by characters of the pubescence and the scales given in the key.

4. ***Alsophila tryonorum*** Riba, *Rhodora* 69: 66, f. 1-4. 1967.

Type: Cuesta de Fusagasugá, Dept. Cundinamarca, Colombia, *Cuatrecasas 8036* (US).

Alsophila tryonorum shows an evident relation with *A. trichiata* because of the similarity of the distribution of the pubescence. However, in *A. trichiata* the rigid trichomes are longer and the catenate trichomes of the petiole are not as abundant as in *A. tryonorum*; the petiole scales in *A. trichiata* have contiguous dark denticulations along the margin, while in *A. tryonorum* the margin has very few dark denticulations or none, except in crozier scales where the dark denticulations are always present. Another relation is with *A. conjugata* based on the similarity of the petiole scales together with the abundant winged trichomes (cf. fig. 2) and bullate scales on the lower surface of the segments. However, the petiole in *A. conjugata* is glabrous, while in *A. tryonorum* it is strongly pubescent with rigid and catenate trichomes.

Alsophila tryonorum (fig. 4) grows in the high mountain forests of northern Venezuela and in the Andean region of Colombia and northern Ecuador.

5. ***Alsophila scabriuscula*** Maxon, *Proc. Biol. Soc. Wash.* 32: 125. 1919.

Type: Cubilquitz, Alta Verapaz, Guatemala, *Türckheim* (J. D. Smith Exsicc. 7806) (US); Isotype (NY).

This species grows in Mexico, Guatemala and Honduras, in the shade of humid tropical forests. Variety ***guatemalensis*** Riba, *Rhodora* 69: 68, f. 8, 1967 [Type: Sierra de los Cuchumatanes, Dept. Huehuetenango, Guatemala, *Steyermark 49417* (F); Isotype: (US)] is confined to central Guatemala.

The differences between the two varieties are in the sinuses and the size of the leaf. In var. *guatemalensis* the sinuses between the segments are acute to narrowly quadrangular, rather than definitely quadrangular, and the leaf

and its parts are smaller than in var. *scabriuscula*. Although the two varieties occur in the same general region they are distinctive in these characters.

6. **Alsophila swartziana** Martius, Icon. Pl. Crypt. Brasil. 73, t. 49. 1834.

Type: based on *Polypodium armatum* Swartz, hence having the same type.

Polypodium armatum Swartz, Prodr. Veg. Ind. Occ. 134. 1788. Type: Jamaica, Swartz (S-PA), photograph and fragment (US).

Alsophila armata (Swartz) Presl, Tent. Pterid. 62. 1836, not *A. armata* Martius, 1834.

Alsophila swartziana is confined to Jamaica, Haiti and Dominican Republic; specimens identified as this species, from Venezuela and Brazil prove to be *A. tryonorum* in Venezuela and *A. hirsuta* in Brazil. *Alsophila swartziana* is closely related to *A. bicrenata*, but that species has the upper surface of the segments glabrous, and the petiole smooth; it also has a close relation to *A. scabriuscula* var. *guatemalensis*, but that variety does not have the characteristic scales between the receptacle of the basal sori and the costule.

7. **Alsophila strigillosa** Maxon, Contrib. U. S. Nat. Herb. 24: 37, t. 11. 1922.

Type: Nima-nima, eastern Cuba, *C. Wright 1062* (YU), fragment (US); Isotype: (GH).

This species has been collected only twice in eastern Cuba. I have been able to examine several sheets of the type collection; besides this, Maxon cites one sheet, *Wright 891* in the Eaton Herbarium (YU), as containing one pinna of *Cyathea arborea* and one pinna of *A. strigillosa*.

Alsophila strigillosa is one of the best defined species of the *Alsophila swartziana* group, as brought out by the characters given in the key. It seems to be related to *A. swartziana* by the similarity of the scale border and margin, and the pubescence of the upper surface of the segments, with just a few stiff hairs on the costule.

8. **Alsophila hirsuta** (Presl) Kunze, *Linnaea* 9: 98. 1834.
Cyathea hirsuta Presl, *Delic. Prag.* 190. 1822. Type: Corcovado, Rio de Janeiro, Brazil, *Pohl* (PR or PRC), fragment (NY).

Alsophila hirta Kaulfuss, *Enum. Fil.* 249. 1824, *ex char.*

This species is known only from Brazil, in some areas of the states of Minas Geraes, Rio de Janeiro, Guanabará, and São Paulo. It is closely related to *A. rufa*, of the same region, differing from the latter by the characters given in the key.

9. **Alsophila rufa** Fée, *Crypt. Vasc. Brasil.* 1: 165, *t. 39, f. 1.* 1869.

Type: Rio de Janeiro, Brazil, *Glaziou 2291* (P).

Alsophila rufa occurs in the same region of Brazil as *A. hirsuta*. The two have sometimes been confused, even considered as the same species, but they are clearly distinct.

10. **Alsophila conjugata** Spruce ex Hooker & Baker, *Syn. Fil.* 37, 1866.

Type: Chimborazo, Ecuador, *Spruce 5745* (K), fragment (US).

This species (fig. 5) is exclusively Andean in distribution, and is the most widely distributed species in the group; it grows from northern Colombia to Bolivia, always in damp forests, ravines, creeks, or along streams, with an altitudinal distribution which varies from 650 m in Peru to 2,800 m in Colombia.

11. **Alsophila stipularis** Christ, *Bull. Herb. Boiss.* II, 4: 958. 1904.

Type: Costa Rica, *Wercklé* (P); Isotype: (US).

Alsophila stipularis grows in the higher mountain regions of Costa Rica and Panama between 1000 and 2000 m. This species seem to be related to *A. conjugata* by the glabrescence of the principal axes of the leaf (petiole, rachis and secondary rachises). The petiole scales, however, are different, having a dark denticulate margin with contiguous dark teeth while in *A. conjugata* the dark teeth are nearly lacking.

12. **Alsophila pansamalana** Maxon, Contrib. U. S. Nat. Herb. 24: 40. 1922.

Type: Pansamalá, Alta Verapaz, Guatemala, *Türkheim* (J. D. Smith Exsicc. 1008) (US).

This species is confined to Guatemala, between 1000 and 2000 m; there is no indication on the collections I have seen concerning the habitat. Its closest relative apparently is *A. scabriuscula* from which it is readily distinguished by its freely armed, glabrous (rather than the scabrous) rachis. The winged trichomes, developed in several species, are illustrated in fig. 2 from the lower surface of a segment.

13. **Alsophila bicrenata** (Liebmann) Fournier, Mex. Pl. Crypt. 134. 1872.

Cyathea bicrenata Liebmann, Dansk. Vid. Selsk. Skrift. V, 1: 289. 1849.

Type: between Trapiche de la Concepcion and Totontepec, Oaxaca, Mexico, *Liebmann* (C), photograph (US); Isotype: (US).

This species is confined to Mexico, from Veracruz to Guerrero, south to Chiapas. It grows in the shade of humid tropical forest, between 1000 and 2000 m.

Alsophila bicrenata is closely related to *A. scabriuscula* var. *scabriuscula*; the petiole scales in both taxa have the same general structure and the habit is very similar. *Alsophila bicrenata* has a glabrous or slightly pubescent petiole, the lower surface of the veins is without long trichomes, and the sinuses between segments are acute or rounded, it has the persistent bullate scales at the base of the costules beneath, these sometimes covering the basal half of the costule.

DISCUSSION.

The differences between the species included in this group are largely in microscopic characteristics, because their gross morphology does not seem to offer characters of specific value. In the whole family, the habit and general morphology are very similar, with a few exceptions. In the

species of the *Alsophila swartziana* group the principal differences are in the type of pubescence and place of attachment of the trichomes. In one species, *Alsophila nesiotica*, the paraphyses are distinctive; in another, *Alsophila estelae*, the venation is distinctive; and in two South American species, *Alsophila conjugata* and *A. tryonorum*, the petiole scales lack the usual dark denticulations on the margin.

The concept of species adopted in this paper is derived from closely related sympatric species in four areas: *Alsophila swartziana* and *A. estelae* in the Greater Antilles, *A. scabriuscula* var. *scabriuscula* and *A. bicrenata* in southern Mexico, *A. tryonorum* and *A. conjugata* in the Andean region, and *A. hirsuta* and *A. rufa* in Brazil. There is no morphological continuity between these species, in each region, and I consider each one of the pair to represent a good species.

To define the distributional center of the group, it is necessary to look for the more primitive species, or at least the less evolved ones. The principal characteristics which are considered as primitive in this group are: a pubescent petiole, a less differentiated border on the petiole scales, and a petiole scale margin without dark denticulations. Accordingly, the most primitive species are the Andean *Alsophila conjugata* and *A. tryonorum*, the latter presenting the most primitive characteristics. *Alsophila trichiata*, Central America to Ecuador, is at about the same evolutionary level.

I suppose, in a purely speculative way, that the distributional center of the species is in the Andean region, an area with many other species of tree-ferns. From this region the migration evidently proceeded north through Central America to Mexico and east to the Antilles. The Antillean species probably were derived from the principal stem which gave rise to the Mexican species. The sympatric groups found in Brazil probably derived from the species of the Andean region, which now has its austral limit in the Bolivian mountains. In regard to *Alsophila nesiotica*, the endemic species

on Cocos Island in the Pacific Ocean, it could be derived from the group represented by *Alsophila trichiata* on the western slope of the Andean region.

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